

NIGERIAN LIZARDS OF THE GENUS *AGAMA*
(SAURIA : AGAMIDAE)



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NIGERIAN LIZARDS OF THE GENUS *AGAMA* (SAURIA : AGAMIDAE)

By ALICE G. C. GRANDISON

SYNOPSIS

The external morphology, distribution and systematics of the species of *Agama* occurring in Nigeria are reviewed. The number and position of the dermal sense organs on the trunk scales are used to help clarify the status and relationships of the five species recognized. *Agama agama benueensis* Monard is shown to be a complex comprising two distinct species, one of which is described as new, the other sympatric with but unrelated to *Agama agama* (Linnaeus). *Agama boensis* Monard is not a valid form; the types are a mixed series of *Agama sankaranica* Chabanaud and *Agama weidholzi* Wettstein.

INTRODUCTION

UNTIL a few years ago it was believed that only three species of *Agama* occurred in Nigeria: the ubiquitous *Agama agama* (Linnaeus) and the two smaller and less common species *A. sankaranica* Chabanaud and *A. gracilimembris* Chabanaud. But in 1963 Dr. Hilary Fry of the Ahmadu Bello University, Zaria drew my attention to the existence of a form which he described as being of similar adult size to *Agama agama* and as occurring on the smaller inselbergs in the Zaria region of northern Nigeria. The adult male was said to be distinguished by four indigo or black, clearly defined blotches on the throat. It was immediately recognized from an examination of an adult male which Fry submitted that this *Agama* was not conspecific with any of the three known species. With the co-operation of members of the staff of his department intensive efforts were made to obtain further examples as well as ecological data. The material resulting from these field studies contained more adult male "blue throats" but not adult females belonging to the same form, instead examples of *Agama sankaranica*, which in the field had been confused with the apparently undescribed form, and gravid females of yet another apparently undescribed agama. The absence in collections of females and immature individuals of this "blue throat" continued until the following year when a Danish zoologist, Dr. Arne Schiøtz, who was working in the British Museum recognized the male blue-throated agama as being similar to ones he had collected in the Western Region. His large series, obtained on inselbergs near Idanre and Igbetti, included both sexes and juveniles and were in the collections of the Zoologiske Museum Copenhagen. A detailed study there of his material enabled me to appreciate the difficulty that other collectors had encountered in the field in distinguishing the females and immature individuals from the superficially similar *A. sankaranica* and to elucidate the intraspecific variation of all the Nigerian forms of *Agama*. The study was extended by referring to type and other material in several institutions and to the British Museum's collections including those acquired during the 1962 Northern Nigeria expedition. Finally the specimens on which Monard based the name *Agama agama benueensis* were borrowed.

The identity and relationships of Monard's *Agama agama benueensis* had not been questioned until Wermuth (1967) in a footnote pointed out that *benueensis* is probably no more than a local variety of *Agama agama agama* differing from it only in minute details of toe length and pattern. The original description of *benueensis*, extremely brief and inadequate, turned out to be based on a mixed series, some of the individuals being conspecific with the Nigerian "blue-throated" form, while others, strikingly different in their pattern and in the position of the nostril and with a lower average midbody count are closely related to *Agama agama* and apparently conspecific with a Nigerian population. The name *benueensis* is here applied to the "blue-throat" form and a lectotype is designated. The information now available on the ecology, morphology, distribution and variation of *Agama agama*, *A. benueensis*, *A. sankaranica* and *A. gracilimembris* is given and a new species is described.

Descriptions are based on the observed variation in the examined material.

Throughout this paper the following abbreviations are used to refer to specimens or collections.

B.M.	British Museum (Natural History)
M.H.N.C.F.	Muséum d'Histoire Naturelle, La Chaux de Fonds
M.N.H.N.	Muséum National d'Histoire Naturelle, Paris
Z.M.C.	Universitets Zoologiske Museum Copenhagen

METHODS AND TERMINOLOGY

The characters used in this study are defined as follows:

Body scales. The shape, size and direction of imbrication of the trunk and flank scales, the extent of the keel relative to the axial length of each scale, from its anterior border to its apex.

Microscopic structure of body scales. The number and position of the "hair-bearing" scale organs on the scales of the mid trunk region were studied by removing a series from the vertebral to the mid ventral row and mounting them according to the method described by Underwood (1957).

Midbody scale count. The number of longitudinal scale rows around the middle of the trunk.

Vertebral count. The number of transverse scale rows along the vertebral line from forelimbs (on a level with the axillae) to hind limbs (groin).

Direction of imbrication of temporal and supratemporal scales. Direction of overlap of the scales in these regions, the regions being defined as: temporal, the area between the anterior rim of the ear and the postocular scales, overlying the temporal fossa and the squamosal and the posterior half of the jugal bones; supratemporals, the scales overlying the supratemporal arcade and the postorbital bone.

Body length. The distance from the tip of the snout to the anterior margin of the vent, measured with dial calipers.

Head length. The distance measured with dial calipers from the tip of the snout to the angle of the lower jaw at the posterior extremity of the articular.

Upper labials. The number of scales bordering the upper lip, counted from the scale adjacent to the rostral to the corner of the mouth.

Lower labials. The number of scales bordering the lower lip, counted from the scale adjacent to the mental to the corner of the mouth.

Lamellae under fourth toe. The number of transversely enlarged scales under the fourth toe from the base of the claw to the junction of the fourth toe with the third toe.

Relative lengths of the toes. Comparisons of the first and fifth and of the third and fourth are expressed as the number of lamellae contained in the difference in lengths when the toes are laid flat and parallel to each other.

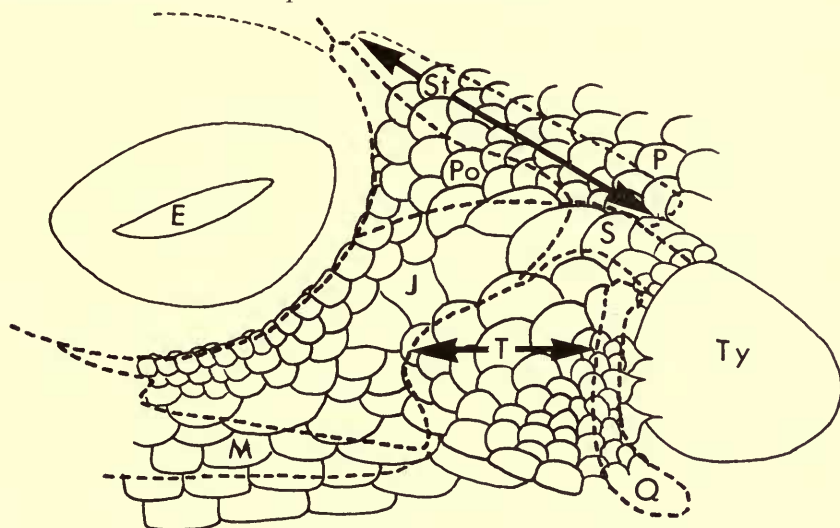


FIG. 1. Supratemporal and temporal areas of *Agama*; underlying bones indicated by broken lines.

E—Eye	Q—Quadrate
J—Jugal	S—Squamosal
M—Maxilla	St—Supratemporal arcade
P—Parietal	T—Temporal fossa
Po—Postorbital bone	Ty—Tympanum

DERMAL SENSE ORGANS

Cohn (1914) was the first person to report on the occurrence of dermal sense organs in *Agama* and he described in detail their histology as well as their external appearance and distribution on various parts of the body. His study was restricted to *Agama colonorum* (= *A. agama*). Subsequently Schmidt (1920) and Preiss (1922) examined the scale organs of other species and genera of lizard, Schmidt extending his studies on reptile receptors to the Gekkonidae, Iguanidae and Agamidae but limiting his investigation of *Agama* to an Asian species *A. sanguinolenta*, which however exhibited several differences from *A. agama*, as described by Cohn, in the number and position of the organs on each trunk scale. It was not until 1937 and 1941 when Scortecci made an extensive survey of the lenticular and "hair-bearing" sense organs in the Agamidae that the density of these receptors and their positions on each scale were shown to have some value as a species character. (The agamid material which

Scortecci used belonged to nineteen genera and eighteen species, his nine species of *Agama* all being African forms but none occurring in West Africa.) But despite the breakthrough afforded by Scortecci's meticulous comparative studies the potential of the receptor character for helping to distinguish agamid species was passed by, yet Underwood (1957) in surveying the scale organs in pygopod lizards had stressed that they would repay further study and Wayne King (1962) had effectively demonstrated their usefulness in sorting out the taxonomy of Caribbean sphaerodactyl geckos. The only attention recently given to these scale organs is by Miller and Kasahara (1967) who have studied their innervation and who remark on the tactile function of the "hair-bearing" receptor.

In species whose mode of life is known correlations might be established between habits and the frequency with which the "hair" bearing organs occur, their position on the scales, their distribution on the body surface and the extent to which the "bristles" project beyond the edge of the scale. An investigation along these lines seems merited but unfortunately through lack of adequate field observations this could not be carried out on West African species of *Agama*.

It has been found in the present study that the species number and the position of the "hair-bearing" organs on the trunk scale do not vary ontogenetically, nor sexually, but that there is some individual variation which is discussed under the species. Nor does this character vary geographically, at least not in four of the Nigerian species where material from throughout their known ranges has been examined. Whether there is geographic variation in *Agama agama* receptors has still to be established but none is evident in the Nigerian specimens.

Another apparently reliable taxonomic character not previously employed in keying out agamas is introduced into this study, namely the direction of imbrication of the temporal and supratemporal scales. These two characters, receptors and direction of imbrication, both of which are probably related to the animal's ecology, seem to have greater significance in classification than some of the characters so rigidly adhered to in the past in keys and descriptions of species of agama; certainly the results of studying them in the Nigerian species are encouraging and an extension of study to other groups of agamid lizards may help elucidate the status and relationships of the many forms that have been described.

Agama agama (Linnaeus)

(Map, Pl. 1, figs. c, d; Pls. 4, 5)

Lacerta agama Linnaeus, 1758 : 207.

MATERIAL EXAMINED. NIGERIA, *Sokoto Prov.*, 1 mile north of Kware, 15 miles north of Sokoto B.M. 1962.1609; *Katsina Prov.*, Rimi village, 13 miles South-east of Katsina B.M. 1962.1608; *Kano Prov.*, Birnin Kudu B.M. 1962.1610; *Bornu Prov.*, Maiduguri B.M. 1962.1611, Galtimare village, South of Maiduguri B.M. 1962.1612; *Zaria Prov.*, Kawo, 4 miles north of Kaduna B.M. 1962.1596-98, Kujama, 25 miles South-east of Kaduna B.M. 1962.1599-1603, Zonkwa B.M. 1962.1604 and 1606, Birnin Gwarri B.M. 1967.2207, Galma Fadama B.M. 1967.2208, Old City Zaria

B.M. 1967.2209-2211, River Amethyst, Kaduna Road, Zaria B.M. 1967.2212; Plateau Prov., Jos B.M. 1962.1613-54, 10 miles south of Jos on Miango Road B.M. 1962.1593-95, Shendam B.M. 1962.1574-92; Oyo Prov., Igbetti Z.M.C. R36561, 36567, 36569, 36573, 36565, 36644, 36655, 36745, 36286-9; Ondo Prov., Idanre Z.M.C. R36577-8, 36584, 36586.

DESCRIPTION. Body subcylindrical, little depressed above, between 3.3 and 3.8 times the head length. The body of adult males rather triangular in section, the apex mid dorsal. Nostril on a line connecting the canthal supraciliaries with the rostral/first labial suture, that is on the canthal ridge; situated in the posterior half or third of a strongly swollen, pear-shaped nasal shield and directed upwards, or upwards and outwards. A keel usually present between the nostril and the anterior edge of the nasal. On its posterior margin the nasal forms a suture, generally a broad suture, with the first canthal supraciliary. The supraorbital scales and the scales overlying the frontal and anterior portion of the parietal quite smooth, the other scales on the head keeled, particularly so in juvenile specimens. The direction of imbrication of the scales overlying the supratemporal vacuity is forwards but the direction of the scales covering the postorbital bone alters to downwards and slightly backwards. The scales overlying the temporal fossa, imbricate in the reverse direction and between the two areas and along an oblique line, which marks the position of the squamosal and the posterior limb of the jugal, is a single row of quite strongly keeled juxtaposed scales (Pl. I, fig. c and Text-fig 1). Occipital enlarged, of variable size, its greatest width generally half to three quarters the diameter of the tympanum. Seven to twelve upper labials; a similar number of lower labials. A long, low nuchal crest of approximately fourteen scales but no dorsal crest. A poorly developed caudal crest present in adult males. The shape of the ear roughly a right-angled triangle, the tympanic membrane rather superficial. No conspicuous fringe of long, pointed scales along the anterior border of the tympanum but a few erect scales which in juveniles may be only slightly raised. A row of erect or somewhat spinous scales from the commissure of the lips to immediately behind and below the tympanum where it joins with one or two (in adults invariably two) *round* groups of spinose scales on the swollen area at the angle of the jaws. At the upper posterior corner of the tympanum a less elevated and more elongated group of erect scales is present. Midway between a point half way along the nuchal crest and the lower posterior corner of the tympanum lies a small oval group of spinose scales; in front of and also behind this group a very small group of erect scales usually insignificant but if prominent the longest scales less than half the width of the tympanum. All these groups of erect scales are considerably more pronounced and the scales longer and more spinous in adult specimens, particularly in adult males, and in the juveniles the groups may be quite inconspicuous. A strong gular fold present in both sexes.

Body scales homogeneous, those in the mid dorsal area flattened dorsoventrally, their distal margins rounded, often only feebly keeled and with short mucrones. Scales on the flanks more rhomboidal, particularly in adult males, the keels more pronounced and terminating in upward turning short mucrones; distal margins somewhat denticulate. Scales on either side of the nuchal crest small, barely mucronate, approximately equal in size to those between the neck pit and ear.

The sense organs of each trunk scale are situated at the distal margin or just below the dorsodistal edge of the scale. They are not confined to the area around the base of the mucrone but may extend along the entire distal aspect of the scale. No scale organ on a trunk scale has more nor less than one "bristle". The number of receptors per scale varies from one to eight and while there is a tendency for the number to increase on the flanks and then diminish towards the venter no definite correlation could be established between the number of organs per scale and the longitudinal scale row although the body scale rows bearing the highest density are invariably between rows ten and sixteen. It is in this region of the trunk that the scales often have a rhomboidal shape with a somewhat denticulated distal margin and each organ is usually situated in an indentation. Harris' (1963) statement that sense organs are absent from the ventral body scales is incorrect. Each ventral scale has one but no more than one "hair-bearing" sensory organ at the apex. The smoother scales of the middorsum generally have one to four sensory organs per scale.

Cohn (1914) found only three organs on each of the scales of the back and describes the central one as placed somewhat to one side of the projecting tip of the keel. He reports a similar number of receptors on flank scales and says that the scales on the vertebral line may lack one or both lateral organs. He gives no indication of the origin of his material which he identifies as *Agama colonorum*, and there seems to be a strong possibility that a misidentification accounts for the much lower density of trunk scale organs in his specimens.

Midbody scale counts of sixty-four Nigerian examples 59-77, the mean for thirty-five females being 68.2 and for thirty males 66.2; vertebral count 38-55. Mature males with eight to twelve, usually ten preanal pores. Eighteen lamellae under the fourth toe. First toe shorter than the fifth by two to seven (usually three to six) lamellae. Third toe shorter than fourth toe by one to two lamellae, very exceptionally subequal. Tail approximately twice the body length, depressed at the base and particularly so in adult males, its scales strongly keeled and mucronate and arranged in whorls.

INTRASPECIFIC VARIATION. Loveridge (1936) in discussing intraspecific variation in *Agama agama* remarked on the extraordinary wide range of midbody count, 60-80, quoted by Boulenger (1885). Presumably Boulenger's counts were based solely on the material that was available in the British Museum at that time, namely twenty-one West African examples many of which bore no more precise locality than "West Africa", and eight Angola and South West Africa examples, in other words a small sample from only a very limited portion of the range of the species. In the 1936 publication Loveridge demonstrated without regard to any sex difference a gradual reduction in the same count from east to west (Uganda to Senegal) and in the belief that populations occurring west of Ghana have a considerably lower average count he suggested recognizing these individuals as belonging to a distinct race, *savatieri* Rochebrune. The recognition of a western race based solely on this character was ill conceived and hasty, particularly in view of Loveridge having at his disposal only one individual from Ghana and none from the 1,000 mile stretch between Ghana and the Cameroun. In 1956 Grandison in reporting on over one

hundred *Agama agama* obtained in West Africa west of Ghana remarked on a south-west to northwest reduction from 68 to 60 in their average midbody count (range of the entire series 56–76). She assigned the individuals to *A. agama savatieri*, having overlooked the statement in Loveridge's later paper (1941) that Hallowell's name *africana* has priority over *savatieri*.

Daniel's (1961) counts (M 61.6 ♂ : 65.1 ♀) on twenty adult Liberian individuals which he identified as *A. agama africana* agree favourably with those given by Loveridge (1936, 1941) for Liberian material but suggest that Loveridge's samples in which the average number of scales round the body was sixty-two probably consisted mainly of males.

The range of variation in midbody count in the sixty-five Nigerian examples studied here runs almost the whole gamut of the variation said to occur in *africana* but the average number of scales in males and females are intermediate between those quoted by Loveridge for Cameroun and Uganda individuals of the nominate form and those given by Loveridge, Daniel and Grandison for examples identified as *africana* and obtained west of Ghana. The Nigerian, Ghanaian and eighteen of the Senegal counts shown in the map are for adult specimens in the British Museum collection.

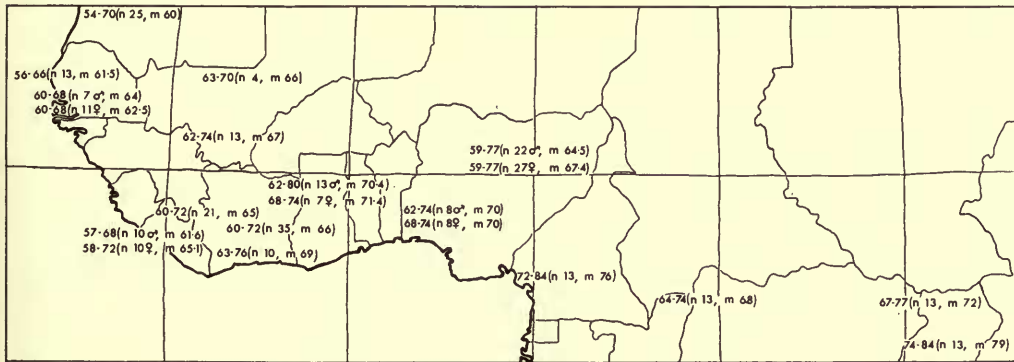


FIG. 2 Geographic variation in midbody count in *Agama agama*.

Thys van den Audenaerde (1963) in his study of Congolese species of *Agama* examined large samples of *A. agama* from the Congo and compared his findings with those of other authors for specimens from all regions in the range of the species. His thorough review of the pertinent literature available on *Agama agama* emphasizes the clinal sequence in midbody count from east to west although his argument is to some extent weakened by blind acceptance of identifications by others, to unequal sampling and to his not distinguishing between the counts for males and for females. He includes in his range of variation in *A. agama* a specimen from the Bauchi Plateau with ninety-two midbody scales that Grandison (1956) identified as *A. sankaranica*. While the individual is not available for re-examination it seems more than likely that it was incorrectly identified and is actually an example of *A. benueensis*, a species closely related to *sankaranica* and in its juvenile livery resembling *sankaranica* but with a considerably higher midbody count. An Air specimen with a

low count of 58 was also mentioned by Grandison (1956) but excluded from the table of means; it too was probably incorrectly identified and may be an example of the large scaled species *Agama boueti* Chabanaud. This species was described from Gao on the Niger. Examination of type material shows that its trunk receptors are similar in number and position to those of *A. bibronii* Duméril of North West Africa and are quite unlike any other West African form.

Thys van den Audenaerde maintains that development of the keel and mucrone is correlated with body count, the lower the count the stronger the keeling, but I can establish no such link in the Nigerian material where variation in this character seems to be related to the proximity of sloughing. He further comments on the geographical variation that occurs in *A. agama* colouration, in particular of the head, throat and tail, which is perhaps correlated with the clinal gradient in scaling and he draws attention to Angolan intermediates between the nominate race and the Angolan race *mucosoensis*. A similar cline in the development of the nuchal crest which both Stejneger (1893) and Thys van den Audenaerde (1963) have suggested exists, has not yet been effectively demonstrated. Much more quantitative data on large samples from throughout the range of the species would have to be compared, sex with sex, if a true picture is to emerge. Meanwhile the only East African figures available are those of Stejneger based on only six Kenya examples, and of Barbour and Loveridge (1928) for eighteen adult Usambara specimens and in neither case is the sex or the proportion of the sexes stated. Since in Nigeria at least, there is a sex difference in the length and height of the crest, the spines being fewer and shorter in the females, the East African figures are not necessarily comparable with those for twenty adult male Nigerian individuals (13-17 : M 14.9).

Thus the abundance of races of *A. agama* that have been described reflects not the occurrence of legitimate geographically localized subdivisions but accidents of sampling or more likely the work of splitters. There would appear to be no evidence of geographic isolates but only of marked individual variation *within* a population and Thys van den Audenaerde's conclusion that *Agama agama* is a large polymorphic species rather than a polytypic species would seem to be the logical one.

COLOUR. Immature individuals and adult females are similar in colouration. In their reproductive colour phase the head is a medium brown or brown with green tinges, the back fawn or brown with darker brown marks of variable shape and position but often in the form of rather indistinct diamond-shaped outlines along the vertebral region. The upper part of the head, the temporal region and the neck have pale green spots and short longitudinal stripes of the same colour. The undersurfaces are a grey-white. Mature males that are dominant over territories are characterized in their reproductive colour phase by an orange head and neck, indigo blue body and by a median orange segment on a black-tipped tail. Other colour phases occur and these as well as the reproductive colour phase are admirably and fully described by Harris (1964).

ECOLOGY. In Nigeria wherever the savanna and forest have been disturbed by human agency, bridges built, houses and shacks erected, trees felled, rubbish dumped, *Agama agama* seems to have established territories. It is very much a commensal

of man and is common around native houses, farm buildings, litter, wood piles and along paths. The species is also common in the boulder strewn country flanking the road from Jos to Miango. Schiøtz (personal communication) says that its habitat preferences do not include flat uniform savanna, nor large rocks, nor dense forest but as soon as such areas acquire human habitations or are in other ways disturbed by man *Agama agama* takes up residence. While this is largely true, the rocky mass of Kujama Hill south of Kaduna supports a number of *Agama agama* yet on the bare rock surfaces of the vast gneiss domes 1,000–3,000 ft. high at Igbetti and Idanre *Agama agama* is absent, its place being taken by *Agama benueensis*.

RANGE. Senegal to Ethiopia, southwards to Tanzania and Angola.

Agama paragama sp. n.

(Pl. 1, figs. a, b; Pls. 4, 5)

Agama agama benueensis Monard 1951 : 131 (part).

MATERIAL EXAMINED. HOLOTYPE: NIGERIA, Zaria Prov., $\frac{1}{2}$ mile Southwest of Ahmadu Bello University, Zaria City, collected by C. H. Fry from Parkia tree on 17.ii.1964, B.M. 1967.2215 ♀.

PARATYPES: NIGERIA, Zaria Prov., same locality as holotype B.M. 1967.2216, Mile 7, Zaria Road B.M. 1967.2214, Mile 5, Zaria Road B.M. 1967.2213, Ahmadu Bello University campus B.M. 1967.2217, no information, probably in vicinity of Zaria City B.M. 1967.2218, Birnin Gwarri, 62 miles Southwest of Funtua B.M. 1968.497, Zaria City B.M. 1968.482–483, Veterinary Unit, Zonkwa B.M. 1962.1605, B.M. 1962.1607; Borno Prov., Potiskum B.M. 1968.498, Yo B.M. 1968.496; Plateau Prov., Naraguta, Jos B.M. 1968.484–485. CAMEROUN, Bangouvé M.H.N.C.F. 1162, Rei Bouba M.H.N.C.F. 1432, 1440, 1459, Mayo Sala M.H.N.C.F. 1374, Ngaouyanga M.H.N.C.F. 965 (six of the paralectotypes of *Agama agama benueensis*.)

These individuals differ from *A. agama* not only in body size, proportions, greater spinosity and in lower average midbody and vertebral counts but in an absence of sexual dimorphism in size. They resemble *A. agama* in the position of the nostril being on the canthal ridge and in having multiple sense organs on the distal edges of the scales of the flanks and the two forms are undoubtedly closely related but being sympatric in Nigeria specific status is given to *paragama*.

Relatively few examples of *paragama* have been collected and the form is so far known only from northern Cameroun and from the Northern Region of Nigeria, although one specimen obtained by C. H. Fry in a crevice 10 ft. up a Terminalia tree in the Botanical Gardens, University College, Ibadan was thought by him to belong to this form; the specimen has not been seen by me. Although situated in the high forest belt Ibadan has many clearings that have the character of cultivated savanna woodland and support typical savanna species. Schiøtz (1963) describes the vegetation of the University College campus as "dry forest and culture savanna". It is possible that where suitable habitats are available this species, like *Agama benueensis*, penetrates the Western Region's forest belt.

DESCRIPTION OF HOLOTYPE. Body subcylindrical, depressed above, 3.6 times the head length. Nostril on the canthal ridge, situated in the posterior half of a swollen, pear-shaped nasal shield and directed laterosuperiorly. Nasal keeled from its anterior tip to the upper rim of the nostril, forming a suture on its posterior margin with the first canthal supraciliary. The supraorbital scales and the scales overlying the frontal and the anterior portion of the parietal quite smooth, remaining head scales keeled. The direction of imbrication of the supratemporal scales is forwards and slightly upwards; anteroventrally the scales overlying the postorbital bone face downwards and backwards. The scales immediately in front of the ear, that is those overlying the temporal fossa, imbricate in the reverse direction to those covering the lower postorbital and between the two areas and along an oblique line marking the position of the squamosal and posterior limb of the jugal is a single row of large, keeled, juxtaposed scales. Occipital enlarged, its greatest width equal to three-quarters the horizontal diameter of the tympanum. Upper labials 8 : 9 (one divided); lower labials 9 : 10. A short but conspicuous nuchal crest formed from nine, long, conical scales, the longest equal to three-quarters the width of the tympanum; no dorsal nor caudal crest. Ear triangular. On anterior margin of ear a fringe of two to three long, pointed scales, on upper posterior border one long, pointed scale surrounded by several erect scales (this group barely developed on left side of head). At the posterior extremity of the lower jaw, that is behind and below the ear, a small, round group of spinose scales of which one scale is three to four times longer than the others. A similar group immediately above. Between a point midway along the nuchal crest and the lower, posterior corner of the tympanum lies a prominent round tuft of long spinose scales the longest scale three-quarters the tympanic diameter; in front (right side only), and also behind, a small, round but insignificant group of erect scales. (The lengths of the scales comprising the nuchal crest and the groups of spinose neck and ear scales are considerably longer and more pronounced in male specimens: see note on variation.) A well developed gular fold.

Body scales homogeneous, the longitudinal rows converging towards the midline, scales on the dorsum and flanks equally strongly keeled and mucronate; the mucrones of the flank scales rather broad at their base, tapering rapidly and rising at an angle to the scale. Distal margins of the body scales rounded on each side of the mucrones. Ventral scales smooth. Scales on either side of the nuchal crest with strong, compressed keels and long, almost erect, mucrones, the scales at least twice the size of those between the neck pit and ear.

The maximum number of sense organs on the middorsal and flank scales is nine, the minimum three. They are situated just under the dorsodistal margin and may extend as far as the "shoulders" of the scale. No scale organ on a trunk scale has more nor less than one "bristle". The highest density of receptors on midtrunk scales occurs on longitudinal rows 3-5. Each ventral scale bears a receptor at its apex.

Midbody scale count 60, vertebral count 30, eighteen lamellae under the fourth toe. First toe four or five lamellae shorter than the fifth toe, third toe half to one lamella shorter than the fourth.

Tail one and a quarter times body length (tip of tail missing), depressed at base,

only very slightly compressed distally, its scales keeled and strongly mucronate and arranged in whorls.

Length of body 94.0 mm.

VARIATION. The following variation in meristic characters in the paratype series was noted. Nigerian individuals: midbody scale count 50–66 (M 58.5), vertebral count 26–34 (M 30.1), number of lamellae under the fourth toe seventeen to twenty-one, first toe shorter than fifth toe by between three and five lamellae, third toe half to two, usually one to two lamellae shorter than fourth toe. Differences in the development of the rosettes of neck and ear spines and in the lengths of the scales forming the nuchal crest are attributable to sex and maturity, in adult males the longest of the pointed nuchal crest scales being as much as equal to the width of the tympanum, likewise the most prominent scales in the neck tufts, whereas in females they are less than three-quarters the diameter of the tympanum. The number of scales forming the nuchal crest varies from eight to ten, the usual number being eight. The density and distribution of "hair-bearing" receptors on the midbody scales of the paratypes is similar to the holotype. Sex dichromatism is discussed below. The tail of the adult male is considerably more compressed than that of the female and has a slight crest; the base of the tail is depressed but not to the same extent as in *Agama agama*.

Juvenile *A. paragama* in which the neck and ear rosettes and nuchal crest are insignificant can be readily distinguished from young individuals of *A. agama* by the relative size of the scales above and below the central neck rosette and by the roundness of the rosette. Further distinguishing features are the pattern, lower vertebral count, gradual tapering of the tail and less depressed base to the tail.

All the Cameroun examples, except an adult male (Mayo Sala M.N.H.C.F. 1374), fall within the range of variation in midbody count of the Nigerian individuals but they have a slightly higher number of transverse rows on the trunk, their vertebral count being 36–38. The Mayo Sala example with seventy-two midbody scale rows is well outside the normal range of variation in the species yet in its other morphological characters it agrees with *paragama*.

COLOUR. Male. In life the upper surfaces of the body and limbs of the adult ♂ are a metallic blue with white flecks. On the back the flecks tend to be arranged in narrow transverse lines, no more than one scale in width, with approximately eight lines between fore and hind limbs. The vertebral zone is whitish, the head chalk white, the proximal two-thirds of the tail whitish, the tail tip black. Except for the whitish areas the general appearance of the ♂ is rather similar to the reproductive colour phase of a male *Agama agama*. Harris (1964) describes in detail the various colour phases of both ♂ and ♀ *Agama agama* and while he refers to a geographical variation in the colour of the head of adult males, northern individuals (Kano) having a deep yellow while more southern populations have either orange or vermilion, he makes no mention of any adult male *agama* in which the orange or yellow tones are replaced by white.

FEMALE. None of the colour phases described by Harris for female *A. agama* occurring in Nigeria corresponds to, or in any way approaches the colour pattern

of female *A. paragama* which is characterized by four or five pairs of more or less clearly defined, large, round, brown spots on a lighter brown (orange in life) background on the dorsum between fore and hind limbs. In those specimens in which the spots are ill-defined the lateral halves of the spots are indicated by narrow, dark brown outlines. The flanks and the upper surfaces of the limbs and tail are of a similar shade of brown to the spots; the head is mottled brown. In both sexes the throat, and in some specimens also the sides of the neck and chest, has a dark network on a cream ground which takes the form of isolated, round, cream spots and is dissimilar to the gular pattern of *A. agama* which tends rather to consist of a longitudinal arrangement of dark lines or blotches (Harris, 1964). The distinctness of the gular spotting does not appear to bear any relation to the maturity or sex of the individual, for example one gravid female has a pronounced pattern while in another a pattern is barely discernible. No pattern whatsoever is present on the throat of one adult male but a distinct network is present in another mature male.

Adult female *paragama* are larger and considerably more robust than female *agama*. Three gravid female *paragama* vary in body size from 96–107 mm. while the gravid female *agama* examined in this study vary from 86–91 mm. Harris (1964) records 97 mm. as the average body length of sixty-eight Nigerian adult female *agama* and Chapman & Chapman (1964) regard all Ghanaian female *A. agama* of about 90 mm. as mature. Adult male *paragama* are considerably smaller (99–108 mm.) than mature male *agama* obtained in the same general area (107–137 mm.).

ECOLOGY. Little information on the ecology of *paragama* is available. Fry (in litt.) states that the species is to be found on the trunks and lower limbs of shade trees and collectors have suggested that it occupies a different ecological niche from *A. agama* but only the specimens collected at Mile 7 Zaria, Potiskum and Birnin Gwarri bear information that suggest an arboreal existence (Mango and Parkia trees); the Yo specimen, a juvenile, was taken on the walls of a house and the rest of the examined material have no biotope data.

RANGE. West Africa: Northern Region of Nigeria to northern Cameroun.

Agama benueensis Monard

(Pl. 2, figs. a–d; Pls. 4, 5)

Agama agama benueensis Monard, 1951 : 131 (part).

Agama agama boensis Monard, 1951 : 130 (part: males).

?*Agama sankaramica*: Grandison, 1956 : 231 (part: Bauchi specimen).

MATERIAL EXAMINED. CAMEROUN, Upper Benue, Ngaouyanga M.H.N.C.F. 956–7, Sakdjé M.H.N.C.F. 1269, Mayo Sala M.H.N.C.F. 1373, Rei Bouba M.H.N.C.F. 1442, 1460, 1517 (seven of the paralectotypes of *A. a. benueensis*), Ngaouyanga M.H.N.C.F. 961 (designated lectotype of *A. a. benueensis*). NIGERIA, Oyo Prov., Igbetti Z.M.C. R 36342, 36345, 36347–51, 36353, 36389, 36392, 36394, 36397, 36399, 36401, 36599, 36601–12, 36614–20, 36661–2, 36702–3; Ondo Prov., Orosuta, Idanre Z.M.C. no number, Idanre Z.M.C. R 36576, 36579, 36580–2, 36585, 36588–9; Zaria

Prov., R. Amethyst, Kaduna Road B.M. 1967.2234-8, B.M. 1967.2263, Ahmadu Bello University campus, Zaria B.M. 1967.2239-44, Siberia, A.B. University campus Zaria B.M. 1967.2254-7, Old City, Zaria B.M. 1967.2245-7, B.M. 1967.2258-61, Mile 5, Zaria Road B.M. 1967.2248-52, B.M. 1967.2253, Zaria B.M. 1967.2262, Near Oomawa, at foot of Kwatarakwashi rock B.M. 1968.490-495; *Plateau Prov.*, Jos B.M. 1968.486-487, Hillcrest School, Jos B.M. 1968.488.

REMARKS. The whereabouts of four of the type specimens of *Agama a. benueensis* (959, 1372, 1441 and 955) listed by Monard (1951) are not known at present. Thys van den Audenaerde tells me he believes that part of the Monard material originally lodged in the herpetological collection at La Chaux de Fonds was transferred to other European institutions and that the missing Cameroun agamas may have been among it. The thirteen individuals from the *benueensis* type series that are available and have been re-examined belong to two morphologically very different forms, and as referred to in the introduction to this paper, the name *benueensis* is applied to the blue-throated form. The other form is described as *A. paragama* sp. n. The Monard specimens here assigned to *A. benueensis* are those males from the Upper Benue that are described by him (1951) as having "une tache noirâtre à la gorge", "une tache foncée à la gorge" and "une raie vertébrale claire", as well as four females and a juvenile male that have a feebly developed pattern characteristic of immature and female Nigerian *benueensis*, and two males from Tibati, Adamaoua Plateau which he assigned to *A. agama boensis*. The Tibati males, M.H.N.C.F. 673, 784, have been examined by Dr. Braestrup who reports (in litt.) that both individuals have chin as well as gular spots. The presence of the gular spots, even if faint, identifies them as *benueensis* for this species is the only West African agama that has a bilobed blotch in this region in the adult male. In the Tibati males the midbody count is about 74, the vertebral counts 45 and 47 which accord with Cameroun examples of *benueensis*. Neither I nor Dr. Braestrup has seen the female, M.H.N.C.F. 726, which Monard also referred to *A. a. boensis* and its identification remains in doubt.

DIAGNOSIS. A large sized *Agama* (body length of ♂ up to 113.0 mm., of ♀ to 74.0 mm.) related to *A. sankaranica* and characterized by a high average number of midbody scale rows, 74-98 (M 88 : N 71) in Nigerian populations, ventrally directed temporal scales and marked sexual dimorphism. Dorsal trunk scales each with one to three single "hair-bearing" scale organs close to base of mucrone, nostril below canthal ridge; in these respects similar to *A. sankaranica*.

DESCRIPTION OF LECTOTYPE M.H.N.C.F. 961, ♂. Body subcylindrical, little depressed above, 3.7 times the head length. Nostril below a line connecting the canthal-supraciliaries with the rostral-labial suture, its aperture round, situated in the posterior third of an elongated, pear-shaped nasal, directed superior-laterally. From the upper rim of the nostril to the front of the nasal shield is a distinct ridge. Canthal-supraciliaries 8 : 9, the anterior forming broad sutures with the nasals at their posterior borders. Supraorbitals quite smooth, supratemporals distinctly keeled, temporals only very slightly keeled. The scales overlying the supratemporal arcade and the postorbital bone directed forwards and slightly upwards; ventrally

the imbrication of the scales covering the posterior part of the jugal, the broad portion behind and below the eye, as well as those over the temporal fossa directed downwards and slightly backwards; no row of keeled juxtaposed scales. Occipital plate enlarged, broadly oval, its length equivalent to the horizontal diameter of the tympanum. Seven to ten upper labials, eight to twelve lower labials. Tufts of enlarged, conical, rather flat scales around the ear, one, consisting of three scales, on the anterior border, one on the upper posterior border, on the lower posterior border a group of about four to five more prominent conical scales and below this group a curved *row* of about five flattish conical scales. At the side of the neck midway between the tympanum and a shallow neck pit, but a little above, a rosette of spines, the longest scale in the rosette two-thirds the length of the nasal. Behind and a little below this rosette and situated above the neck pit an oblique or vertical line of conical scales. Above and slightly behind the tympanum a prominent erect scale surrounded by a few lower but erect scales. Ear subtriangular, its horizontal diameter equal to the distance from the tip of the snout to the middle of the nasal. A gular pouch present. Nuchal crest low, formed from about ten conical scales; no dorsal nor caudal crest. Dorsal scales imbricate, homogeneous, strongly converging on the vertebral line, strongly keeled but the keel not markedly compressed, mucrone finely tapering, ventrals and subcaudals smooth.

A maximum of two scale organs on each body scale but usually only one and situated under the dorsodistal edge of the scale close to the base of the mucrone. Each scale organ bears a single "hair".

Midbody scale count 78; vertebral count 46; preanal pores in two transverse rows, 13 anteriorly, 15 posteriorly. The adpressed hind limb reaches to posterior border of the tympanum. Nineteen lamellae under the fourth toe. First toe three or four lamellae shorter than fifth toe, third toe one lamella shorter than fourth toe.

Tail slightly depressed at the base; broken. Caudal scales keeled and mucronate, arranged in distinct whorls.

Body size 94.0 mm.

COLOUR IN ALCOHOL. Apart from a conspicuous whitish vertebral line approximately three scales wide and extending from the nape to the base of the tail there is little colour pattern discernible. Any pattern that may have been present on the flanks of the living animal has become obscured by preservation and sloughing and only a slight mottling of cream and dark brown is now evident. The throat bears a large, blackish, bilobed patch at the level of the gular fold; in front of this patch and extending on to the chin are several small, dark spots on a cream background. The rest of the undersurfaces are a grey-cream.

COLOUR IN LIFE OF NIGERIAN EXAMPLES. Dorsum grey or brown with whitish dark-edged ocelli on the flanks which are arranged in two or three longitudinal rows, the spots in the outer, or middle in the case of individuals with three rows on each side, generally larger than the others. Across the back from the shoulders to the tail a series of dark chocolate brown bands which, particularly in juveniles, are considerably broader and often diamond-shaped on the vertebral line and enclose a narrow, longitudinal, whitish streak. The streaks become confluent in some adult

males and females (see sex dimorphism) and form a diffuse yellowish vertebral stripe. Schiøtz (personal communication) describes the entire dorsum and belly of adult males as having a distinct bluish tinge, but not of such an intense blue as the *Agama agama* dominant male, while the chin and throat are yellow with two to four dark blue or black patches. The upper surface of the male's head is irregularly mottled green; the tail is greenish with indistinct yellow bands.

The ground colour of the female varies according to the colour of the rocks or soil in its habitat. At maturity the transverse bands on the trunk are reddish brown and the sides of the head are greenish. The ventral surface of both the female and the juvenile is white but the chin and gular region of most individuals has a network of dark lines forming irregular spots.

INTRASPECIFIC VARIATION. An analysis of meristic variation in the material examined shows some geographical differences. The samples from the western region (Igbetti and Idanre) have the highest midbody and vertebral counts, midbody 84-98 (M 91.3 : N 34), those from the Jos Plateau and the Cameroun the lowest, 68-82 (M 76 : N 11) while the gradation in the Zaria Province population almost spans these two extremes, 74-96 (M 85.8 : N 34). The variation in these characters for the entire series is : midbody 68-98 (M 87.0 : N 79), vertebral 41-56 (M 48.6 : N 76). The correctness of the identification of the individuals at the extremes of the variation is not in doubt, a combination of other characters such as throat markings, position of nostril, trunk scale organs and direction of imbrication of the post-orbital/temporal scales assigning them unquestionably to *benueensis*. Variation in the number of fourth toe lamellae (nineteen to twenty-three) and in the relative lengths of the first and fifth, and third and fourth toes is independent of the variation observed in midbody and vertebral counts and appears to have no geographical nor ontogenetic significance. The third toe may equal the fourth but generally it is shorter by half to one lamella. Variation in the relative lengths of the first and fifth toes is greater; the first is always shorter than the fifth but the difference may be as many as four lamellae.

In the majority of the examples studied the lateral head scales between the eye and the ear all imbricate downwards or downwards and slightly backwards but in a few individuals, juveniles as well as adults, the scales in the lower posterior quarter of this area, that is those overlying the temporal fossa are directed forwards and upwards, in other words in a similar direction to those of *Agama agama*; however they are not as strongly keeled as in *agama* nor are they separated from the post-orbital/supratemporal scales by an oblique row of juxtaposed scales.

Scales on either side of the nuchal crest are not or only slightly mucronate and are only slightly keeled. They are considerably larger than the scales below the central group of spines on the side of the neck.

SEXUAL DIMORPHISM AND DICHROMATISM. Some sexual dichromatism is evident, notably in the conspicuous gular and chin spots which are a characteristic feature of the adult male. The twin gular spots develop before the chin spots and first appear as a darkening of the median gular region which later becomes an intense black or navy bilobed blotch; occasionally the lobes are separated on the midline.

The gular spots do not develop until the male reaches a body size of over 73 mm., although there is one exception among the fifty-six males examined, a 69.7 mm. individual collected at Igbetti. By 80 mm. most of the males have developed two additional dark spots; these are on the chin and somewhat oval and parallel to each other on either side of the median line. The development of these gular and chin spots in adult male *benueensis* does not seem to be seasonal; they are present in Nigerian individuals collected in January, February, March, June, July and August. The three largest males in the Cameroun series (72.5, 78.3 and 74.0 mm.) which were obtained in July and in September have only gular spots.

Adult males retain some evidence of the juvenile pattern; generally the two longitudinal rows of ocelli along each flank are discernible, although feebly, as well as remnants of the five dark transverse lines in the mid dorsal region on each side of the midline from shoulders to groin but the light coloured vertebral streaks, a characteristic feature of the juvenile livery, invariably coalesce and form an ill defined light vertebral zone extending from the nape to the tail. The female sample is insufficient to be certain whether a similar light vertebral zone always develops at maturity. Only six of the fifteen females are gravid and of these six only the two Cameroun examples (M.N.H.C.F. 1460, 1269) have a clearly defined continuous light line. In the other examples the vertebral pattern is obscure in all but one of the Igbetti examples (Z.M.C. 36351). In both sexes the dorsolateral series of ocelli becomes progressively less distinct as the individuals mature. Egg bearing females were obtained in July, August and September. Preanal pores are usually ten to twelve in a single series but in three Idanre males, the only male *benueensis* collected there, and in the lectotype the pores are in double series 13 + 14, 10 + 13, 8 + 13, 13 + 15 respectively.

ECOLOGY. In the western region of Nigeria Schiøtz (personal communication) says that *A. benueensis* is strictly confined to large rocky outcrops such as the vast gneiss inselbergs where it is common both in the savanna (Igbetti) and in the forest (Idanre). Other ecological niches that he searched in southern Nigeria, such as mounds of boulders, small rocky areas, produced no examples. He noted that *benueensis* hides in rock crevices and among vegetation at the perimeter of an inselberg but conducts its feeding and sexual activities on the actual surface of the rock. Farther north on the Jos Plateau the species is much less abundant but it is again quite common in Zaria Province on the inselbergs around Zaria City as well as in a variety of other habitats such as on mounds of laterite on open farmland in the Galma Fadama, a locality some miles from the nearest inselbergs, on sandy river banks (Amethyst River) and in sandy stream beds (R. B. Walker, personal communication). Near Sabon Gari, in an area of scrap cars and garbage tips, both *A. benueensis* and *A. agama* were taken and no specific habitat preference was noted but Schiøtz maintains that at Igbetti *A. benueensis*, *A. sankaranica* and *A. agama* can be seen virtually only a few feet from each other yet each still adhering to its preferred habitat.

A careful search by Schiøtz of the Shai Hills in Ghana and suitable localities in the Eastern Region of Nigeria failed to produce any *benueensis* and he believes the species

may also be absent from the Bamenda region of the Cameroun. *Agama benueensis* seems to be endemic to the Western and Northern regions of Nigeria and the upper Benue valley in the Cameroun.

Monard (1951) does not record the biotopes for the type series of *benueensis* and he describes only the general areas around the villages. The 1 : 1,000,000 maps of the Upper Benue show the villages where *benueensis* were taken as being in an area deeply dissected by the Benue and its tributaries and at altitudes varying from 740 ft. to 1,400 ft.; only Ngaouyanga is on a high steep-sided wooded platform, the other localities are in or at the sides of valleys in woodland savannah.

RANGE. West Africa: Western and Northern Regions of Nigeria and northern Cameroun.

Agama sankaranica Chabanaud

(Pl. 3, figs. a, b; Pls. 4, 5)

Agama sankaranica Chabanaud 1918 : 105.

Agama boensis Monard 1940 : 155 (part: adults only).

MATERIAL EXAMINED. PORTUGUESE GUINEA, Madina Boé M.H.N.C.F. 865, 867-8 (three of the syntypes of *Agama boensis*). REPUBLIC OF GUINEA, Beyla M.N.H.N. 21.309-316, Kankan M.N.H.N. 21.297-298, Kerouané M.N.H.N. 21.299-308, B.M. 1921.11.12.1-5. MALI, Moussaia, Sankaran M.N.H.N. 1901.395 (holotype of *Agama sankaranica*). GHANA, B.M. 1930.6.9.8 Korley Bu, Accra B.M. 1931.5.6.3, B.M. 1932.6.1.5-7, Tamale B.M. 1927.9.27.199, Tafo B.M. 1962.910. NIGERIA, *Benue Prov.*, Makurdi B.M. 1937.12.4.14; *Plateau Prov.*, Shendam B.M. 1962.1573; *Kano Prov.*, Kano B.M. 1961.2069, B.M. 1962.567 (no. 567 later skeletonized); *Zaria Prov.*, B.M. 1967.2206, Rimi, South-east of Kaduna B.M. 1962.1572, Zonkwa B.M. 1962.1571, Ahmadu Bello University campus, Zaria B.M. 1967.2205, 14 miles South of Zaria B.M. 1967.2204; *Lagos Prov.*, Lagos B.M. 1960.1.7.28; *Oyo Prov.*, Igbetti Z.M.C. R 36386, 36388, 36390, 36393, 36395-6, 36398, 36403, 36405, 36407, 36597, 36607, 36697-8, 36691, 36758.

DIAGNOSIS. A medium sized *Agama* (body length of adult males averaging 66 mm., of mature females 76 mm.) belonging to the group of agamas that have the nostril below the canthal ridge, homogeneous scaling and dermal sense organs not exceeding three in number on each trunk scale. Related to *Agama benueensis* Monard but distinguished by a lower average midbody count (69.6) and by dorsally directed temporals scales.

DESCRIPTION. Body subcylindrical, scarcely depressed above, 3-3.7 times the head length. Nostril below the canthal edge, situated in the posterior half of a slightly swollen, oval nasal, directed laterally. No post nasal separating the first canthal supraciliary from the nasal. Scales of the head keeled; the interorbital scales considerably smaller than the supraorbitals; imbrication of temporals directed upwards and of supratemporals directed upwards and forwards (Pl. 3 fig. b) Occipital large, its greatest width equivalent to or as much as one and a half times greater than the diameter of the tympanum. Eight to twelve upper labials; a

similar number of lower labials. Usually three tufts of long, conical spines on posterior border of ear; behind and above these a single group of spines and yet farther back and just above a shallow neck pit another group of somewhat shorter spines. A weakly developed gular pouch. A low nuchal but no dorsal or caudal crest. Dorsal scales homogeneous, broadly rounded, strongly keeled and mucronate, the sharp high keel extending the length of each scale, the mucrone very slender. Scales on the flanks slightly smaller than dorsals, similarly keeled and mucronate. Ventrals keeled only in juveniles. "Hair-bearing" sensory pits on the dorsal midtrunk scales confined to around the base of the mucrones, at or just under the dorsodistal edges of the scales. The maximum number of scale organs on each scale is three but invariably no more than two are present. In the vertebral region at midbody there are generally two "hair-bearing" pits, each with a single hair-like projection, the one pit close to the base of the mucrone or under the mucrone and concealed in dorsal view, the other on the opposite side of the mucrone but near the apex of the scale. On more lateral scales there is a tendency for only the more lateral, that is lateral with respect to the mucrone, to develop.

The number and position of the scale organs on the dorsal scales bear a close similarity to the condition obtaining in East African *rueppelli* and described and figured by Scortecci (1937). Midbody scale count 64-78 (M 69.6 : N 61); vertebral count 32-46 (M 38.8 : N 61). Mature males with eight to twelve usually ten preanal pores in a single transverse row. Fifteen to twenty-one lamellae under the fourth toe. First and fifth toes subequal or first toe one lamella shorter. Third toe usually subequal to fourth toe, rarely half to one lamella shorter or longer than fourth. Tail one and three quarter times the body length, depressed at the base, slender and cylindrical distally, its scales strongly keeled and very distinctly mucronate, not arranged in distinct whorls.

COLOUR IN ALCOHOL. Upper parts reddish brown. Invariably a conspicuous yellowish or russet vertebral stripe from behind the head to the proximal third of the tail, much broader and always prominent in the cervical region but narrowing rapidly to a width of approximately two scales on the rest of the body. On each side of this stripe and from nape to tail broad, dark brown, transverse bands, six between the nape and hind limbs. At the lateral extremities of these bands light-coloured ocelli or elongated blotches which in some specimens coalesce to form a light dorsolateral stripe. In some examples the vertebral stripe widens at the level of each transverse band to form light diamond-shaped areas. Halfgrown individuals occasionally have indistinct marbling on the flanks below the ocelli or dorsolateral stripe. In one mature male, collected at Zaria, the transverse bands are broken up into irregularly shaped blotches. Between the eyes a thin dark transverse line is present; four similar lines radiating from the eyes to the lips are usually evident. Limbs indistinctly cross-banded with narrow dark lines.

SEXUAL DIMORPHISM. There are no obvious external differences between the females and immature males. Adult males have eight to twelve preanal pores and also broken, longitudinal, blue stripes on the chin and throat which become more prominent with maturity and often enclose a large, dark blue, median gular spot

and a lozenge-shaped chin blotch. The rosettes of neck spines and the lips may also be blue in mature males. Adult females are on average rather larger than adult males. The body length of mature females varies from 68–85 mm. (average 76.2 mm.) while males vary from 62–76 mm. (average 66.4 mm.).

REMARKS. The examined material consists of examples from throughout the known range of the species. No evidence of geographical variation can be demonstrated. The examples from the extreme west of the geographical range of *sankaranica* are the three adults, two males and one female, in the series of syntypes of *Agama boensis* Monard. These individuals unquestionably belong to *sankaranica*. The throats of the males have the blue blotches and stripes that are typical of mature male *sankaranica*, furthermore the scale counts and other morphological characters including the density and distribution of trunk receptors agree well with *sankaranica* although one male with a midbody count of 64 is exceptional in having 20 : 21 lamellae under the fourth toe, which is outside the range for all other specimens examined (fifteen to nineteen). The fourth syntype of *boensis*, a juvenile, lacks a nuchal crest and clusters of neck spines and has a single apical scale organ on each body scale; it is conspecific with *Agama weidholzi* Wettstein. (Grandison, in press.) The Cameroun individuals assigned by Monard (1951) to *A. a. boensis* are discussed in the section on *A. benueensis*.

ECOLOGY. In the field this species has often been confused with female and immature *Agama benueensis* and as a result some ecological information claimed to be on *A. sankaranica* has had to be disregarded or treated with suspicion in this study. Dr. Arne Schiøtz' reliable field notes and comments make it clear that he readily distinguishes *sankaranica* from *benueensis* and his notes correspond with my own field observations in stating that unlike all other Nigerian species of *Agama*, with the exception of *gracilimembris*, *sankaranica* does not form family groups but is a solitary creature. The species has been observed and captured in ploughed farmland and in maize and cassava plantations when running along the rutted ground, also on paths in grass covered savanna. Schiøtz' notes state that he saw the species on the ground only in grass covered savanna or in rather dense tree savanna and never in forest nor on rocks. The localities at which examples of *A. sankaranica* have been collected are, with one exception, in the Doka and True Guinea woodland belts from Nigeria westwards to Portuguese Guinea; the exception is an individual taken at Kano which is towards the southern limit of Sudan woodland.

RANGE. West Africa: Portuguese Guinea to Nigeria.

Agama gracilimembris Chabanaud

(Pl. 3, figs. c, d; Pl. 6)

Agama gracilimembris Chabanaud, 1918 : 106.

MATERIAL EXAMINED. DAHOMEY, M.N.H.N. 04.114–5 (syntypes). NIGERIA, *Benue Prov.*, Lafia B.M. 1938.3.1.47, Wukari B.M. 1938.3.1.48–9; *Plateau Prov.*, Shendam B.M. 1962.1570; *Zaria Prov.*, Zonkwa B.M. 1961.949, B.M. 1962.1569, Samaru Bush, Zaria (on exchange to Vienna Mus.); *Oyo Prov.*, Igbetti Z.M.C. R 36654, R 36701, R 36263; *Kano Prov.*, Kano B.M. 1961.2067–8, B.M. 1962.566, CENTRAL

AFRICAN REP., " Pays des Senoussi " M.N.H.N. 17.191 (according to information received from Dr. J. Guibé this specimen was collected in the neighbourhood of Ndellé, 8° 25' N : 20° 36' E).

DIAGNOSIS. A small sized *Agama* (body length of males up to 47 mm., of females to 57 mm.) lacking tufts of erect spiny scales behind the ear and bearing only one receptor on each body scale, related to *Agama weidholzi* Wettstein but distinguished by heterogeneous body scales, strongly keeled head scales and a low fourth toe lamellar count (13-14).

DESCRIPTION. Body slightly depressed, 3-3.6 times the head length. Nostril below the canthal edge, situated in the posterior half of a convex, often keeled, oval or pear-shaped nasal; directed laterally. Interorbital scales as large or larger than the supraorbitals. Above the nasal a continuous series of three clearly defined, somewhat elongated scales runs from the rostral to the canthal-supraciliaries. The first canthal-supraciliary is separated from the nasal by a small postnasal. Scales of the head strongly keeled, somewhat rugose; imbrication of temporal scales directed downwards and slightly backwards. Occipital large, its greatest width equivalent to the diameter of the tympanum. Nine to twelve, usually ten upper labials; eight to eleven, usually ten lower labials. No tufts of spines around the ear, instead single, short, conical scales close to the border of the ear and three to four tubercles on the side of the neck in a slightly curved row extending from the upper edge of the ear to above a point midway between the neck pit and the arm insertion; additional tubercles irregularly scattered below this row and between the ear and the neck pit, the lowest at the jaw angle. No gular fold. No trace of a nuchal or dorsal crest. Dorsal scales heterogeneous, those in the vertebral region a little larger than the lateral series; on the flanks, and irregularly disposed, some large scales which are as big and occasionally bigger than the vertebrales.

The scales of the midtrunk region broadly oval or pear-shaped with pronounced " shoulders ", dorso ventrally flattened on each side of a high keel, the edges of which rise abruptly from the scale. The keel extends half to two-thirds the length of the scale but does not project beyond the scale apex to form a mucrone. A single sensory organ is present on the dorsodistal surface of each of the midbody scales just under the keel tip or very slightly to one side and sometimes evident only when the scale is viewed from behind. Generally each of these organs bears one but never more than one " hair ", which projects slightly beyond the apex of the scale and by macroscopic inspection may be mistaken for a mucrone. Gular and ventral scales strongly keeled. Midbody scale count 70-85 (M 74.8 : N 16) vertebral count 30-46 (M 37 : N 15). Mature males with eight to twelve preanal pores in a single transverse row. The adpressed hind limb reaches to the tympanum. Thirteen to fourteen lamellae under the fourth toe. The first toe is usually either one lamella longer than the fifth toe or equal to it; rarely (two examples) is it shorter (half lamella). The third toe exceeds the fourth toe in length by half to two lamella. Tail one and a half times the body length, depressed at the base, slender and cylindrical distally its scales strongly keeled and slightly mucronate, and not arranged in whorls.

Body length of gravid females 49.0-56.7 mm., of mature males 44.0-47.0 mm.

COMPARISON OF CHARACTERS OF NIGERIAN SPECIES OF *Agama*

	<i>agama</i> *	<i>paragama</i> *	<i>benueensis</i> *	<i>sankaranica</i>	<i>gracilimembris</i>
Dorsal body scales	Homogeneous	Homogeneous	Homogeneous	Homogeneous	Heterogeneous
Position of nostril	On canthus	On canthus	Below canthus	Below canthus	Below canthus
Dorsal body scales keeled and mucronate	+	+ (strongly)	+	+ (strongly)	Keeled but not mucronate
Keeled ventrals	—	—	—	+ (juveniles only)	+
Midbody count	59-77 (M68.2 ♀ : M66.2 ♂)	50-66 (M58.5)	74-98 (M91.3 W.R. : M85.8 Zaria)	64-78 (M69.6)	70-85 (M74.8)
Vertebral count	38-55 (M46)	26-34 (M30)	42-56 (M50)	32-46 (M39)	30-46 (M37)
Nuchal crest	+	+	+	+	—
Imbrication of scales in temporal region on left side of head	↘ ↗	↘ ↗	↘ (rarely) ↗	↗	↘
Number of receptors per dorsal scale	1-8	3-9	1-2 (rarely 3)	1-2 (rarely 3)	1
Keeling of dorsal head scales	Faint	Faint	Faint	Keeled	Strongly keeled
Fourth toe lamellae	18-25	17-21	18-23	15-21	13-14
First to fifth toe (difference expressed in number of lamellae)	<(3-6)	<(3-5)	<(3-4)	Subequal	<(½), = or >(1)
Third to fourth toe	= or <(1-3)	<(½-2)	= or <(½-1)	= or <(1) or >(1)	>(1-2)
Body length of gravid ♀	84-91 mm.	96-107 mm.	65-74 mm.	68-85 mm.	49-57 mm.
Body length of adult ♂	107-137 mm.	99-108 mm.	80-113 mm.	62-76 mm.	44-47 mm.
Tufts of spines behind ear and on side of neck	+	+	+	+	—

* Based on Nigerian individuals only.

COLOUR IN ALCOHOL. ♂ Upper surfaces of body and limbs greyish brown; usually a clearly defined light vertebral stripe which extends from behind the occiput to the base of the tail. Straddling the vertebral stripe from nape to base of tail are nine < > shaped, dark chocolate brown marks which in some specimens are rather obscure. In the same region and alternating with these marks, diamond-shaped brick orange zones occasionally present. The lips, snout, supraorbital and tympanic and parietal regions invariably dark brown or blue black but a lighter area over the occipital is always present. Dark, irregular, longitudinal lines are usually present on the throat, chest and belly but they may extend no farther backwards than the gular region. In a sexually mature male these lines are dark brown and closely set to give a brownish appearance to the entire belly; the throat has a dark median area.

♀ The entire dorsal surfaces of the body, tail and limbs brown with obscure, irregularly placed lighter areas. An ill defined light vertebral stripe occasionally present. Snout, supra-orbital area, cheeks and oblique stripe from below eye to commissure of lips dark brown; occipital, temporal and nuchal regions light fawn. Above and behind each ear a large ill defined blackish patch in which the small pointed scales stand out clearly as light bluish or greyish spots. Lower surfaces greyish white with faint longitudinal dark lines from throat to belly. In some specimens these lines do not extend farther than the chest.

ECOLOGY. *A. gracilimembris* is the rarest of the West African savannah species and has been recorded from only a few localities all of which are in the Doka and True Guinea woodland vegetation belts and on the extreme southern limit of Sudan woodland (at Kano). Its biotope has not been described.

RANGE. West Africa: Dahomey to Ubangi Chari.

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Summary of taxonomic changes:

<i>Agama boensis</i> Monard part	= <i>A. sankaranica</i> Chabanaud
<i>Agama boensis</i> Monard part (juvenile)	= <i>A. weidholzi</i> Wettstein
<i>Agama a. benueensis</i> Monard part	= <i>A. benueensis</i> Monard
<i>Agama a. benueensis</i> Monard part	= <i>A. paragama</i> sp. n.

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PLATE 1

- a. *Agama paragama* sp. n. Holotype B.M. 1967.2215.
- b. *Agama paragama* sp. n. Lateral view of the head of the holotype.
- c. *Agama agama* L. Lateral view of the head of a juvenile female B.M. 1967.2212.
- d. *Agama agama* L. Dorsal view of same individual.

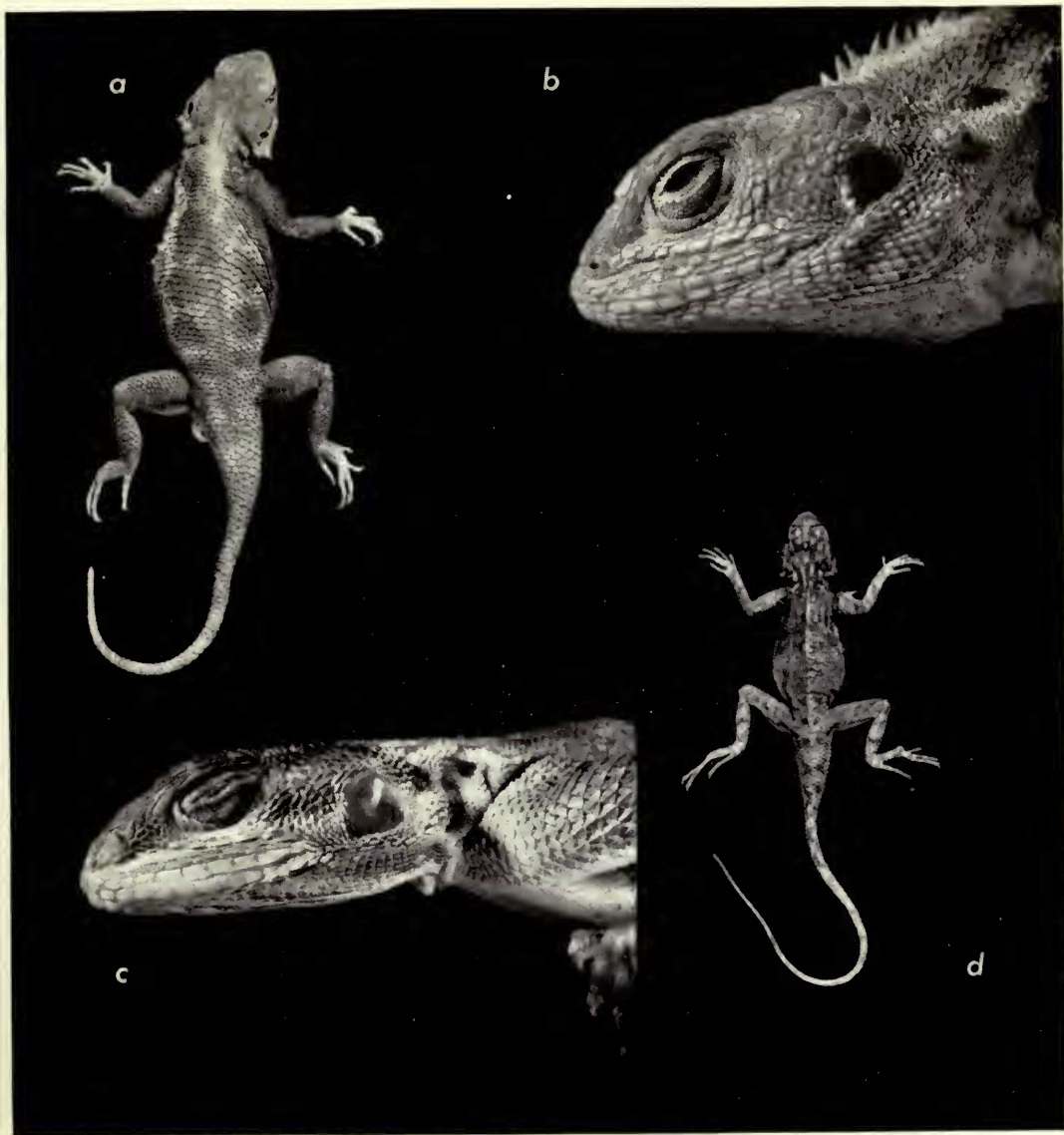


PLATE 2

- a. *Agama benueensis* Monard. Dorsal view of an immature male B.M. 1967.2239.
- b. *Agama benueensis* Monard. Dorsal view of an adult male B.M. 1967.2234.
- c. *Agama benueensis* Monard. Throat of a sexually mature male B.M. 1967.2253.
- d. *Agama benueensis* Monard. Lateral view of the head of an immature male B.M. 1967.2239.
Note developing dark gular patch.

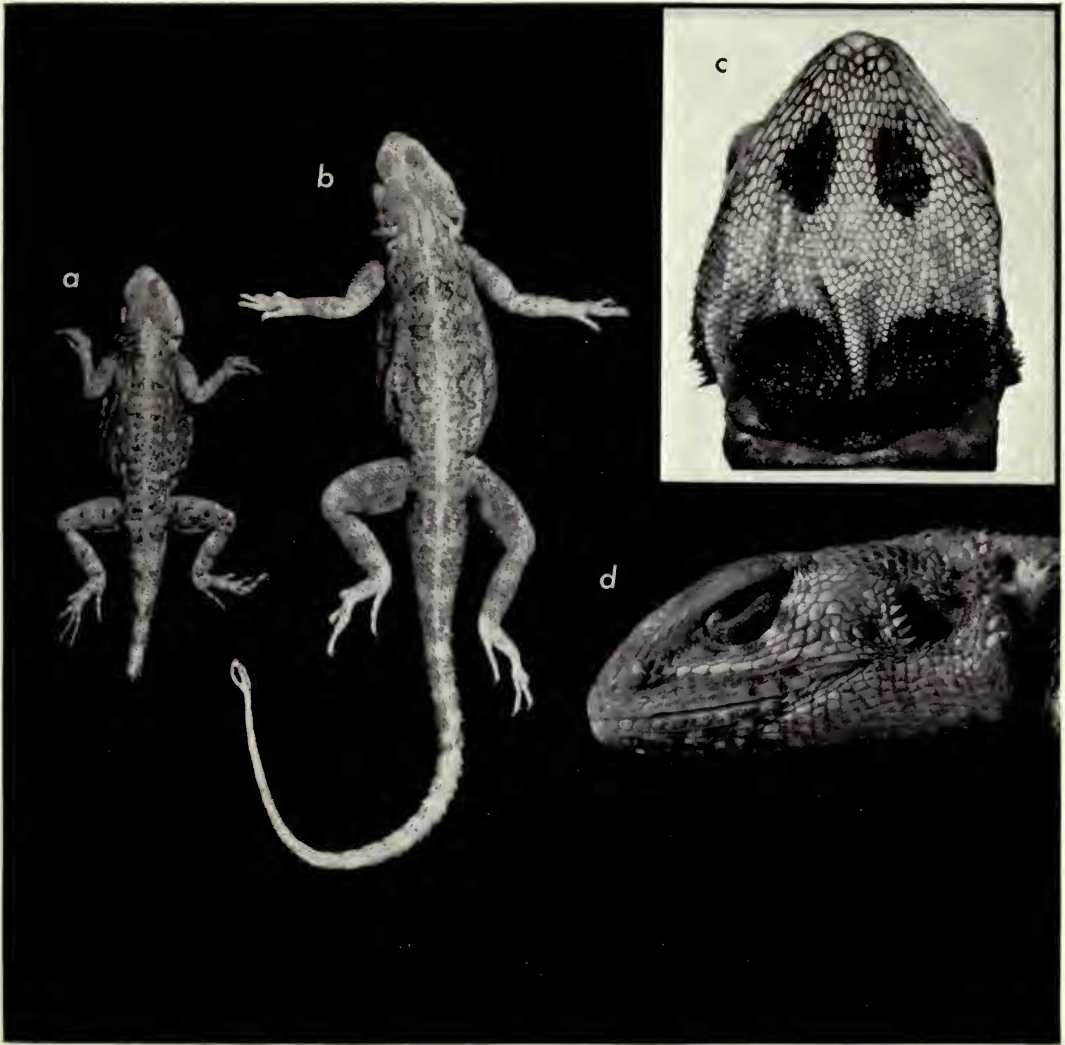


PLATE 3

- a. *Agama sankaranica* Chabanaud. Dorsal view of an adult female B.M. 1967.2204.
- b. *Agama sankaranica* Chabanaud. Lateral view of the head of the same individual.
- c. *Agama gracilimembris* Chabanaud. Lateral view of the head of an adult male B.M. 1961.949.
- d. *Agama gracilimembris* Chabanaud. Dorsal view of same individual.

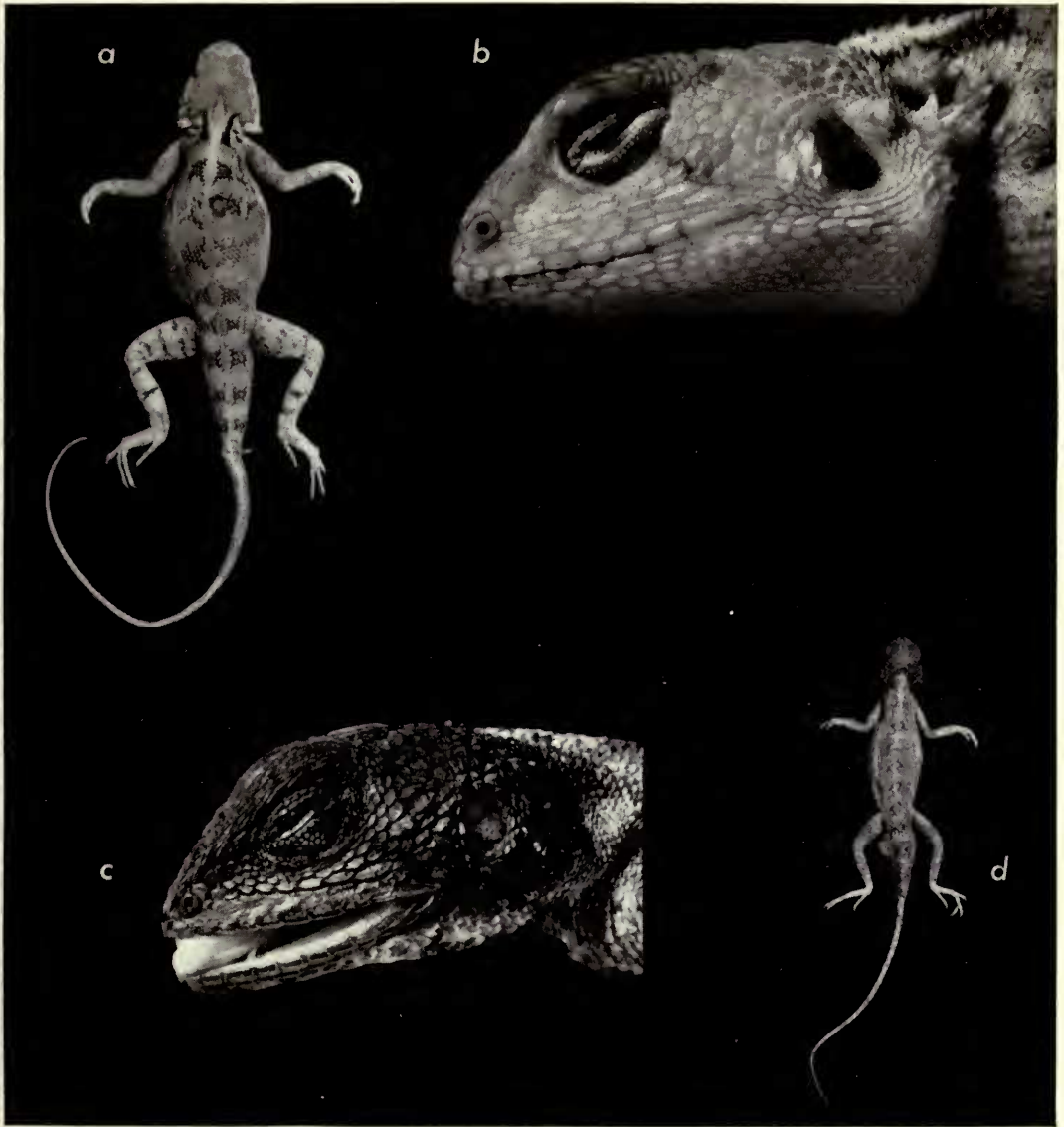
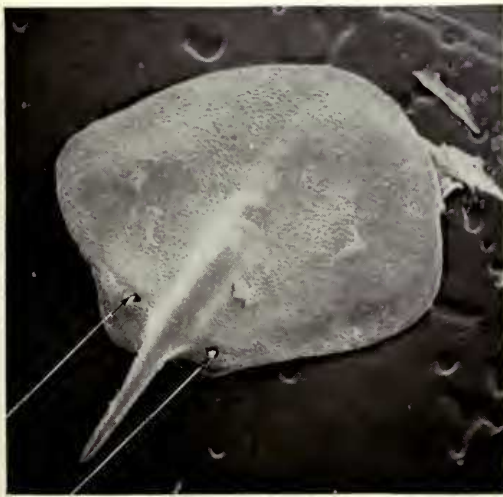
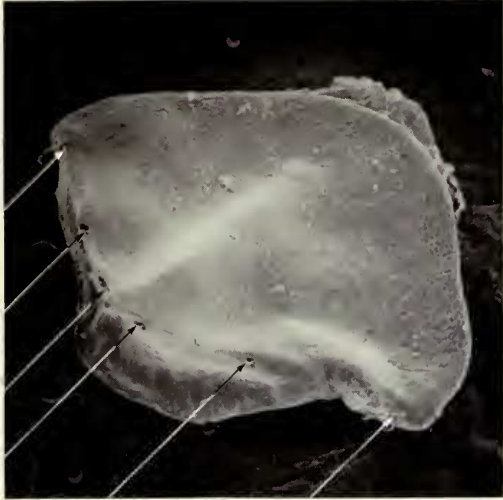


PLATE 4

Stereoscan electron microscope photographs of dorsal midbody scales. Arrows point to the sense organs.

Upper row left to right.	<i>Agama agama</i>	B.M. 1962.1595 × 48
	<i>Agama paragama</i> sp. n.	Holotype × 28
Lower row left to right.	<i>Agama bemeensis</i>	B.M. 1967.49 × 52
	<i>Agama sankaranica</i>	B.M. 1967.2204 × 47



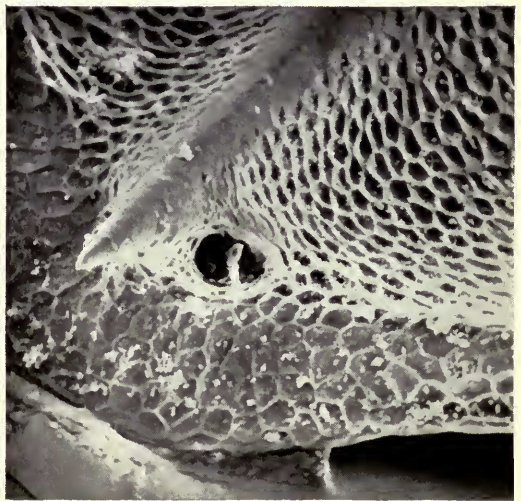
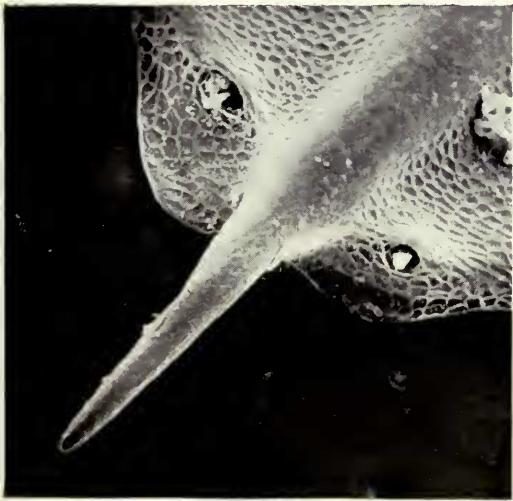
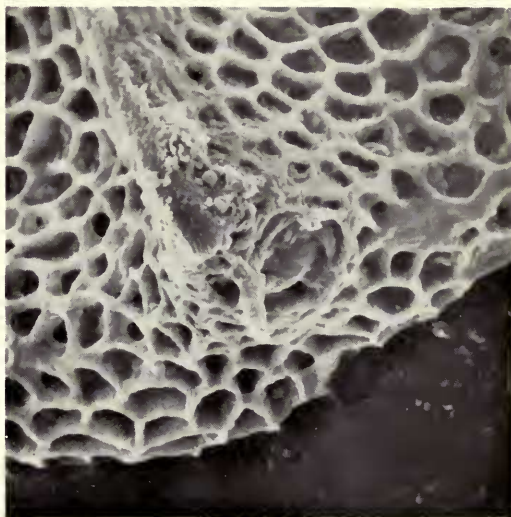


PLATE 6

Stereoscan electron microscope photographs of a dorsal midbody scale of *Agama gracilimembris* B.M. 1961.949 showing the position of the single "hair-bearing" sense organ directly below the termination of the keel.

Left $\times 110$.

Right $\times 580$.



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